

Ontogeny of the Commissure of *Equisetum*

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The genus *Equisetum* is characterized by having whorled leaves fused into a nodal sheath. This sheath consists of a variable number of segments, or leaves, three in *E. scirpoides* to 50 or more in *E. giganteum*. Each segment has a single vascular bundle, continuous with a vascular bundle of the internode below it, and is terminated by a tooth, or free leaf tip. Between adjacent segments there is an anatomically distinct commissure.

This commissure was first described by Duval-Jouve (1864) as consisting of transversely elongated cells at the bottom of the commissure bordered by oblique to irregular cells, as opposed to the vertically elongate cells of the sheath epidermis. Milde's (1867) description was a little more complete. There is a row of transversely elongated cells lying one above another, which have strongly thickened walls. Their ends bend a little downward, giving them a half-moon shape. Neighboring cells overlap them, and this overlapping may be so strong as to completely cover the cells of the commissure. Müller (1888) provided an extended discussion of the commissural appearance. He named the transversely oriented row of cells "anchor cells" (*ankerzellen*) because they anchor the adjacent sheath segments. With the adjacent obliquely oriented cells they form parabolic curves he compared to "chain lines" (*kettenlinien*), which are formed by suspending a chain between two upright supports. With descriptions, mathematical formulae, and polarized light analyses of cell walls, he supported his theory that the characteristic form of the commissure is the result of rapid elongation of the sheath teeth stretching the still meristematic cells of the commissural region.

He described the appearance of the commissure in cross-section and the variation between species. The anchor cells have swollen ends and thick walls. They are underlain by small, thick-walled cells of the inner epidermis. In some species the commissure is shallow, in others deep, and in some the sides of the commissure overhang the furrow and partly to completely occlude it.

Mature anchor cells bend at the ends transversely outward. The wall is thick, but thinnest at the bend. According to Müller this makes the commissure stretchable. The sheath functions to protect the growing point and developing sheaths, and its stretchability allows them to elongate through it, and provides flexible protection and mechanical strength for the intercalary meristems at the base of the internode above the sheath.

Müller (1888) described the ontogeny of the anchor cells in *E. hyemale*. At the commissure the young cells are 2-4 layers thick, descended from one or two meristem cells. Over them lies a single, large, somewhat 6-sided cell, which belongs to the outer epidermis. The inner wall is about twice as long as the outer wall. The lateral neighbors of the anchor cell are meristematic and divide, so

that the sides overgrow the anchor cell, until the commissural groove is a mere slit (Fig. 15). The outer wall of the anchor cell becomes as big as the inner wall. Just under the anchor cell a cell is cut off, either from the underlying cells or from the anchor cell itself, which may divide once or more, and which forms a pillow for the anchor cell. Finally the ends of the anchor cell grow out and gradually bend around, forming the anchor shape. Then the walls become thick, and thus is established the deceptive appearance of an anchor cell lying deep in the inside of a closed tissue complex. The nucleus of the young anchor cell is larger than those of the adjoining cells and is elliptical. As the cell ends grow out, the nucleus remains right in the middle of the lengthwise axis, coming to lie against the outside wall and becoming spindle-shaped. According to Müller the rhizome sheaths have no such distinctive commissure.

Schellenberg (1895) disagreed with Müller, and attributed the characteristic appearance of the commissure to unequal growth at the base rather than teeth enlargement. He pointed out that the teeth have elongated before the commissure forms. The lower part of the sheath segment is more actively growing than is the lower part of the anchor cell row. Upper cells of the anchor cell row accommodate this unequal growth by stretching into parabolic curves. Sadebeck (1902) described the establishment of the anchor cell row by division from the neighbor cells. As the sheath grows, it forms new anchor cells, but only from below. He cited Müller's explanation of tooth growth causing stretching of cells.

More recent authors have not described the commissure. DeBlock (1923) speaks of the sheath segments being "conrescent," Eames (1936) describes the leaves as "fused laterally," Smith (1955) says they are "laterally united," Bierhorst (1971) calls them "connate," and having "a single row of hook-shaped cells that seem to clamp the adjacent leaves together," Foster and Gifford (1974) say they are "united," and Bold et al. (1980) "fused."

I (1979) observed variations in appearance of the commissures of species of subgenus *Equisetum*, and have since studied the anatomy and ontogeny of the commissure of *Equisetum*. The distinctive row of cells in the middle of the commissure will be called the C-cells here, short for commissure, rather than anchor cells, which implies a function which may be misleading.

MATERIALS AND METHODS

Buds of *Equisetum arvense*, *Equisetum diffusum*, *E. hyemale*, and *E. telmateia* were killed and fixed in FAA, transferred to 70% EtOH, dehydrated in a tertiary butyl alcohol series, embedded in Paraplast, (mp 56–57°C) and sectioned on a rotary microtome at 10 μm (longitudinal sections), or 20 μm (transverse sections). These were stained with aqueous ferric chloride and tannic acid (the reverse of the usual sequence of Foster, 1934), counterstained with .01% toluidine blue in 95% EtOH, and mounted in Diaphane. Some fixed buds were cleared with 10% KOH followed by chloral hydrate, stained with tannic acid and ferric chloride, teased apart in Diaphane and mounted on slides. The photos were taken on Kodak Plus-X or Technical Pan film with a Nikon Microflex UFX camera mounted on a Zeiss microscope. Sources of plant material are as follows:

Equisetum arvense.—Moat in front of main library, University of Rhode Island campus, Kingston, 31 Aug 1974 (Voucher: Hauke 514, KIRI).

E. diffusum.—Pot in University of Rhode Island, Botany Department greenhouse, Kingston, 10 Jan 1985. Plant originally collected near Simla in Himchal Pradesh state, India (Voucher: Hauke s.n., KIRI).

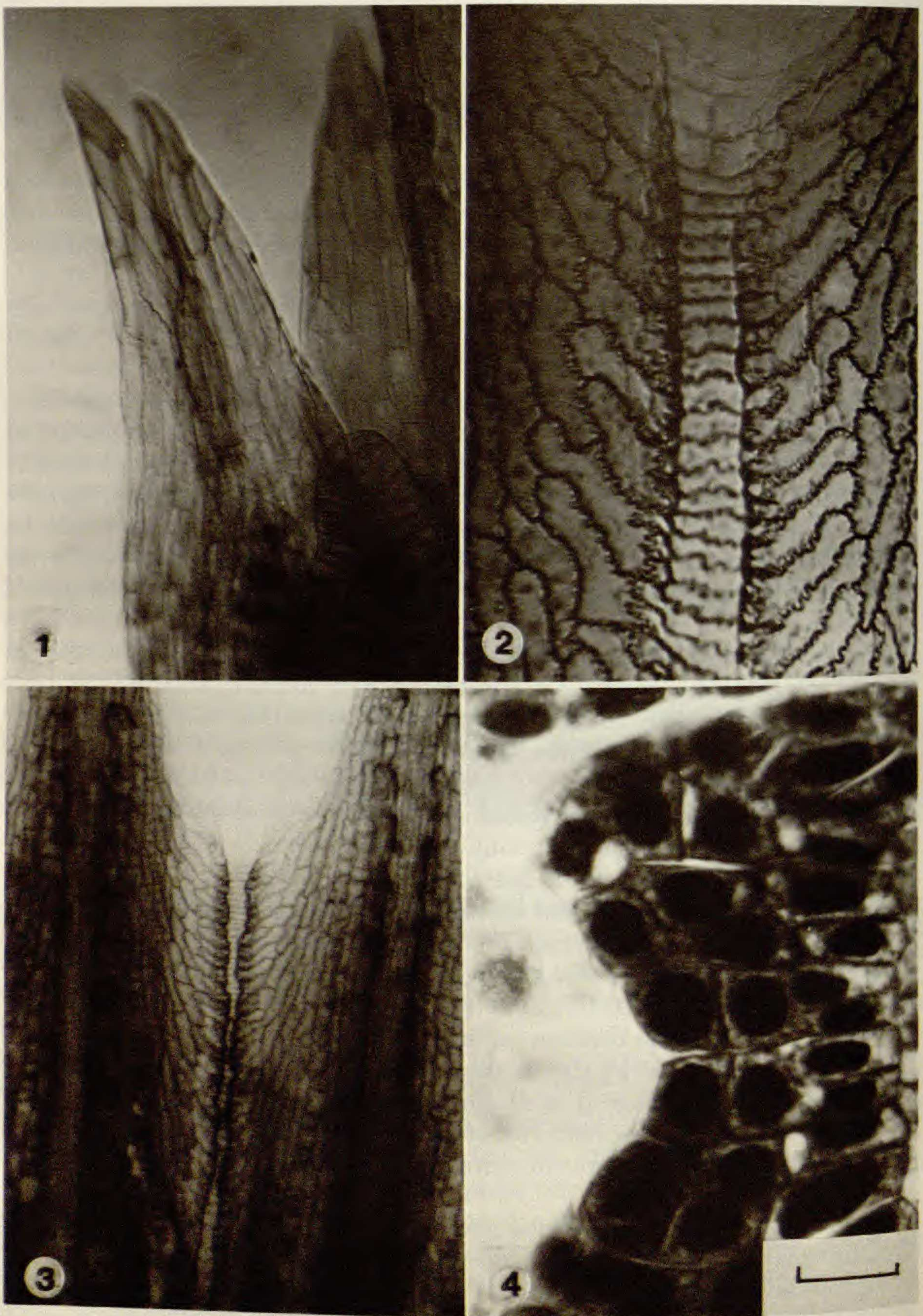
E. hyemale.—Northeast corner of Galilee Escape Rd. and Great Island Rd., Narragansett, Rhode Island, 31 Dec 1984 (Voucher: Hauke 515, KIRI).

E. telmateia.—South side of Claremont Ave., just E of Alvarado St., Oakland, California, 4 Dec 1980 (Voucher: Hauke C1, KIRI).

RESULTS

From the cleared material of *E. diffusum*, it was apparent that the sheath teeth enlarge and mature before there is much development of the lower portion of the sheath (Fig. 1). Such clearings also showed dramatically the mature form of the commissure, with its row of C-cells and oblique lines of neighboring cells (Figs. 2, 3). Longitudinal sections confirm what the clearings suggested, that the three youngest sheaths are primarily growing by tooth development, that the fourth and fifth youngest sheaths show rapid growth of the basal, fused part of the sheath and the commissures, and that the sixth and older sheaths have maturing or matured C-cell rows. The youngest sheaths do not show any median line of cells (Fig. 4). The earliest appearance of a median line is 4 large cells appearing approximately square in tangential sections (Fig. 5). The number increases until there are 10 or more square to slightly rectangular cells (Fig. 6). In cross-section of the sheath (Fig. 7) these cells can be seen as trapezoidal, so that an abaxial longitudinal section would appear square, whereas the adaxial section would appear rectangular. I could not determine whether the C-cell row originated by one or more of the pre-commissure sheath cells assuming a more median position, by longitudinal division of pre-commissure cells to create a median line of cells, or in some other manner. Once the row is present, the number of cells in it greatly increases by transverse division (Fig. 9) and the cells become more rectangular to tangentially elongated. That the increase in number of C-cells is by transverse division throughout the row rather than by basal initial activity is also indicated by the relation between the C-cells and the adjacent cells. At the cuboidal stage (Fig. 6), the two are about the same height. In the rectangular stage there are often two or more C-cells for each neighbor cell (Fig. 8). In the tangential stage, three or more C-cells may abut a single neighbor (Fig. 10).

Whereas the C-cells are dividing only transversely, the neighboring cells are dividing obliquely (Fig. 8, arrow) and thus establishing the oblique orientation of the adjacent cells. Adaxial to the C-cell row is an inner epidermis of vertically elongated cells. There may be two or more side-by-side under a given C-cell (Fig. 6, arrow), and each may be longer vertically than two C-cells (Figs. 11, 12). As the C-cells mature, they bend outward at the ends (Fig. 13) to achieve the shape of a letter C in transverse section. This bending causes a deep furrowing of the commissure in *E. diffusum* (Fig. 3).



FIGS. 1-3. *Equisetum diffusum*, clearings of sheaths. FIG. 1. Branch tip with young sheath showing precocious teeth elongation. Scale bar = 80 μm . FIG. 2. Commissure of C-cells and adjacent oblique cells. Scale bar = 50 μm . FIG. 3. Adjacent sheath segments with prominent commissural furrow. Scale bar = 200 μm . FIG. 4. *Equisetum diffusum*, tangential section, young sheath before initiation of C-cell row. The apex of the sheath is toward the left. Scale bar = 20 μm .

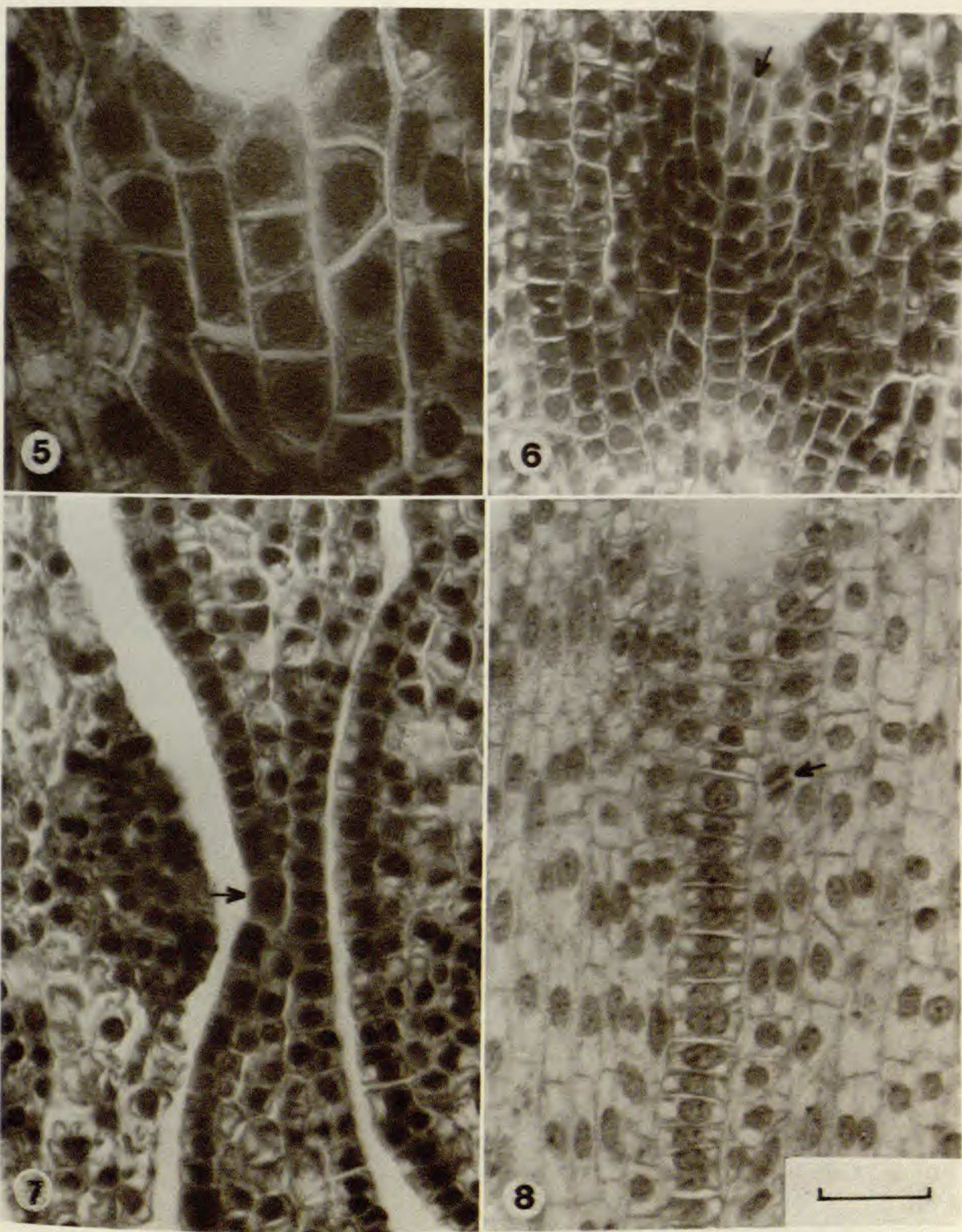


FIG. 5. *Equisetum diffusum*, tangential section, earliest visible C-cell row, of 4 cuboidal cells. Scale bar = 20 μm . FIG. 6. *Equisetum diffusum*, tangential section, C-cell row of more than 10 rectangular cells. Arrow indicates the underlying adaxial epidermal cells, taller than the C-cells and two abreast. Scale bar = 50 μm . FIG. 7. *Equisetum arvense*, cross-section, sheath with trapezoidal C-cell (arrow) underlain by adaxial epidermal cells. Scale bar = 50 μm . FIG. 8. *Equisetum telmateia*, tangential section, C-cell row of numerous rectangular cells. Arrow marks oblique division figure in a neighboring cell. Scale bar = 50 μm .

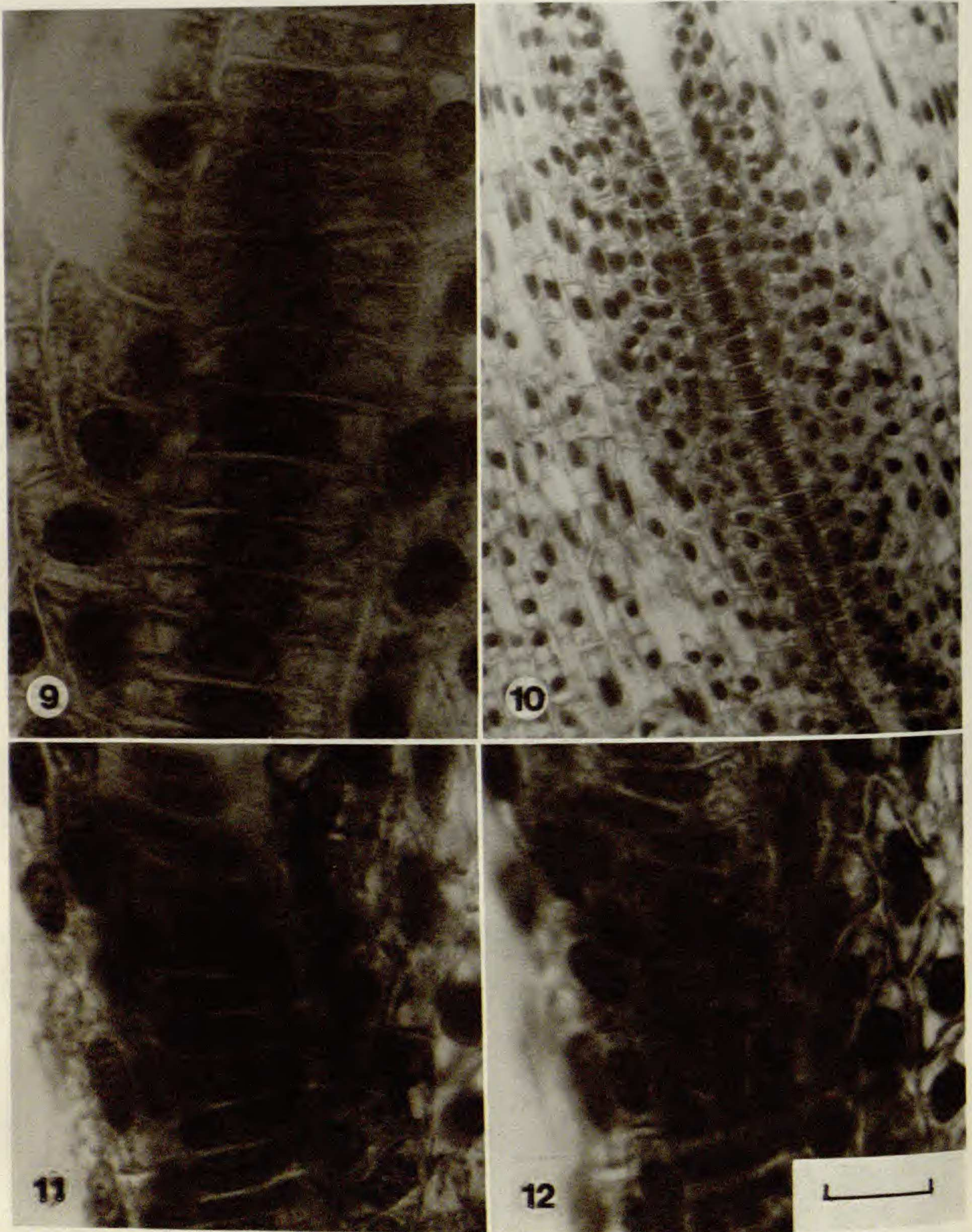


FIG. 9. *Equisetum telmateia*, tangential section, C-cell undergoing transverse division. Scale bar = 20 μm . FIG. 10. *Equisetum arvense* tangential section, commissure with C-cells tangentially elongated. Scale bar = 80 μm . FIGS. 11, 12. *Equisetum diffusum*, tangential section, two optical sections showing the C-cell row of tangentially elongated cells underlain by adaxial epidermal cells which are vertically elongated and narrower than the C-cells. Scale bar = 20 μm .

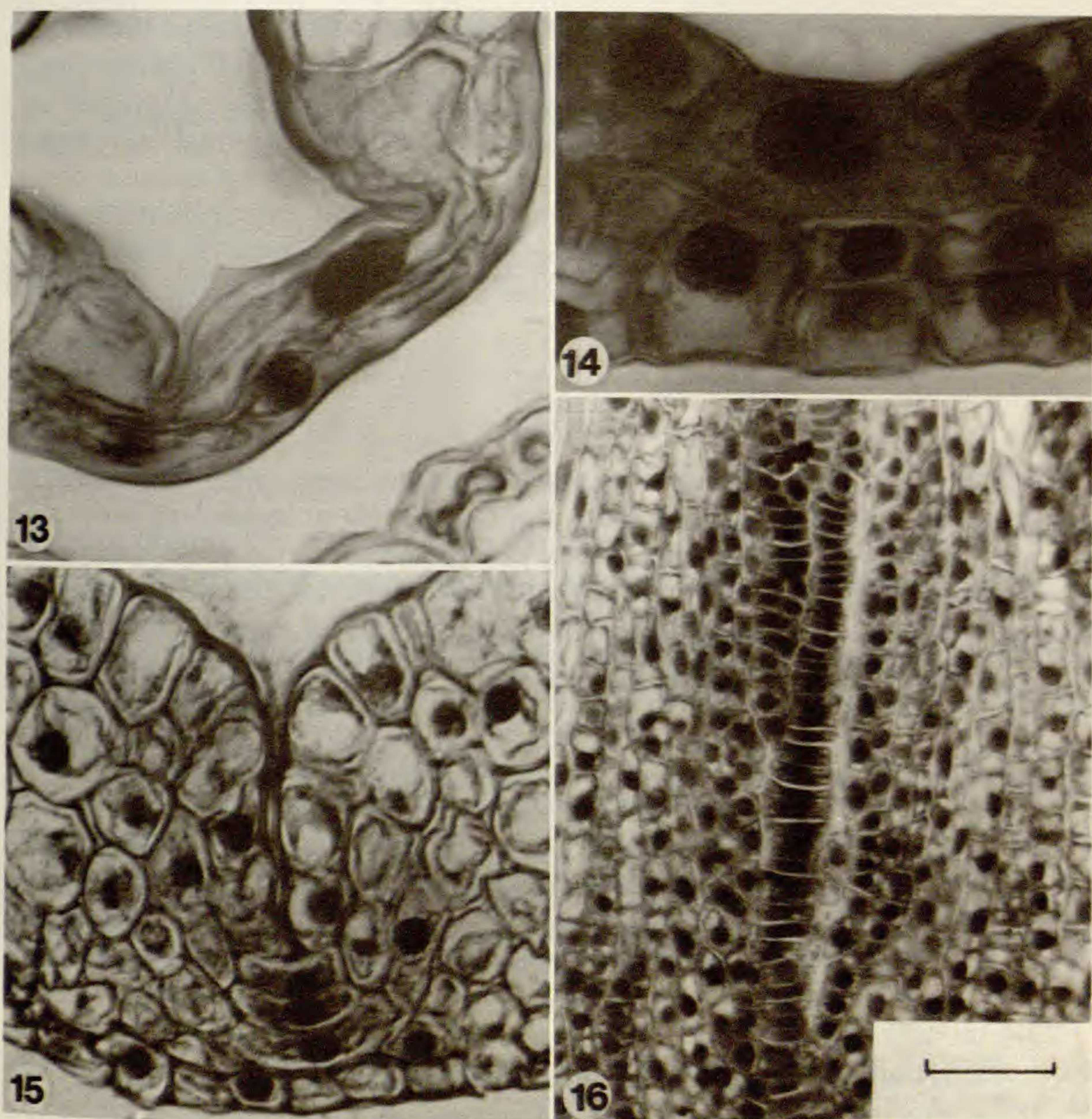


FIG. 13. *Equisetum diffusum*, cross-section, C-cell with prominently bent ends. Scale bar = 20 μm .
 FIG. 14. *Equisetum telmateia*, cross-section, commissure with adaxial epidermis proliferated by periclinal division. Scale bar = 20 μm . FIG. 15. *Equisetum hyemale*, cross-section, commissure of C-cells occluded by growth of neighboring cells. Scale bar = 50 μm . FIG. 16. *Equisetum diffusum*, tangential section, rhizome commissure showing less-ordered structure. Scale bar = 80 μm .

The ontogeny described here for the commissure of *E. diffusum* was also seen in *E. telmateia*. In that species, however, periclinal division of the adaxial layer (Fig. 14) in the basal part of the commissure made it multilayered. *Equisetum arvense*, also studied for comparison, does not develop as deeply furrowed a commissure as do the above two. Because of its occluded commissure, *E. hyemale* does not show the distinct C-cell row with oblique adjacent cells characteristic of *E. diffusum*, and was not studied developmentally. At maturity (Fig. 15) it does appear to be occluded by overgrowth of adjacent cells, as described by Müller (1888) and to have formed "pillow" cells by periclinal division of the C-cell.

The nucleus of the C-cell is particularly noteworthy. It is always prominent and remains in the center of the cell (Figs. 8, 9, 14). As the cell changes from cuboidal to rectangular to tangential, the nucleus becomes more extremely ellipsoidal. As the cell folds outward, the horizontally attenuated nucleus remains in the center portion (Fig. 13).

The distinctive commissures described are from aerial stems, or branches. The rhizome sheath commissures are apparently much less regular in their development (Fig. 16), for the C-cells do not form a single distinct, uniform row, nor do the adjacent cells form "chain lines."

DISCUSSION

Although Müller's (1888) description of the commissure, with its distinctive median row of abaxial epidermal cells, the C-cells (his *ankerzellen*) was accurate, his "chain line" explanation for the oblique appearance of adjacent cells by stretching caused by growth of the sheath teeth, was not. Schellenberg (1895) attributed them to unequal growth at the base, which is more nearly correct. Actually, the characteristic appearance is the result of control of plane of division. In the median row, cell division is always transverse, and there is little subsequent elongation of daughter cells. Hence from a row of a few initially cuboidal cells is produced a longer row of rectangular cells, and eventually a very long row of tangentially elongate cells. This transverse division activity occurs throughout the C-cell row, and there is no basal initial, as Sadebeck (1902) implied. The cells adjacent to the commissural row divide in various plants, including obliquely, to produce the parabolic curves with C-cells at the apex. The distinctive outward bending of the C-cell, and the equally distinctive appearance and position of the nucleus cannot be explained here.

Since the sheath grows as a unit from an initial ring produced just below the apex, descriptions of the sheath segments as "con crescent," "fused," or "united" are misleading. These terms could be understood to indicate ontogenetic rather than phylogenetic fusion. The term "connate" is preferable, since it means literally "born together" and indicates congenital fusion.

LITERATURE CITED

- BIERHORST, D. W. 1971. *Morphology of vascular plants*. New York: The Macmillan Co.
- BOLD, H. C., C. J. ALEXOPOULOS, and T. DELEVORYAS. 1980. *Morphology of plants and fungi*. 4th ed. New York: Harper & Row.
- DEBLOCK, L. 1923. Contribution à l'étude des Equisétacées. Thesis. Faculty of Medicine & Pharmacy, Lille.
- DUVAL-JOUVE, J. 1864. *Histoire naturelle des Equisetum de France*. Paris: Bailliere et Fils.
- FOSTER, A. S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. *Stain Tech.* 9:91-92.
- and E. M. GIFFORD. 1974. *Comparative morphology of vascular plants*. 2nd ed. San Francisco: Freeman.
- HAUKE, R. L. 1979. A taxonomic monograph of *Equisetum* subgenus *Equisetum*. *Nova Hedwigia* 30:385-455. (1978)

- MILDE, J. 1867. *Monographia Equisetorum*. Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 32(2):1-605 + 35 pl.
- MÜLLER, C. 1888. Über den Bau der Commissuren der Equisetenscheiden. *Jahrb. Wiss. Bot.* 19: 497-575.
- SADEBECK, R. 1902. Equisetaceae. Pp. 520-548 in *Die natürlichen Pflanzenfamilien*, Vol. 1(4). eds. A. Engler and K. Prantl. Leipzig: Verlag Engelmann.
- SCHELLENBERG, H. C. 1895. Zur Entwicklungsgeschichte der Equisetenscheiden. *Ber. Deut. Bot. Ges.* 13:165-174.
- SMITH, G. M. 1955. *Cryptogamic botany II. Bryophytes and pteridophytes*. 2nd ed. New York: McGraw Hill.

REVIEW

"*Ferns of Jamaica, a Guide to the Pteridophytes*," by George R. Proctor. 1985. vi + 631 pp. British Museum (Natural History). ISBN 0-565-00895-1. £50.00.

The publication of a complete new pteridophyte Flora for a tropical country is always a major event. Jamaica, being a small island (11,424 km²; 4411 mi²) with high mountains (up to 2250 m elevation) and varied topography and soils, supports an unusually large pteridophyte flora (609 taxa, 82 (13.3%) of them endemics) for its size. The *Ferns of Jamaica* is unique in that the author resided in Jamaica for many years. He made extensive field surveys and collections and saw almost all the taxa as living plants. This contrasts greatly with other Floras, which are by necessity based largely on herbarium specimens with occasional trips to the field by the authors. Thus, the habitat data given by Proctor are unusually complete and helpful, and even serve to amplify the distinctions between closely related species like *Pityrogramma williamsii* Proctor (on calcareous earth banks and limestone boulders) from the similar appearing *P. sulphurea* (Swartz) Maxon (on non-calcareous earth banks). The well-written keys, brief descriptions, and habitat and frequency statements make this Flora easy and pleasant to use; one could read it cover-to-cover for the pleasure of discovering the many original ecological observations. Some of the species of each genus are illustrated, often by reproducing graceful line drawings found in 19th century works on ferns. The taxonomic concepts are broad at all levels, but subcategories are freely employed. The book is the capstone and monument to the productive years that Proctor spent in Jamaica, but it is by no means a culmination: he is currently preparing a Flora of the pteridophytes of Puerto Rico and the Virgin Islands, to which he has added dozens of species new to the Flora as a result of intensive fieldwork and a consummate knowledge of Antillean Pteridophyta.—DAVID B. LELLINGER, Department of Botany, National Museum of Natural History NHB-166, Smithsonian Institution, Washington, DC 20560.